Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration[a)]

Thomas F. Norris[b)]
8455 Kingsland Road, San Diego, California 92123

Mark Mc Donald
2535 Sky View Lane, Laramie, Wyoming 82070

Jay Barlow
Southwest Fisheries Science Center, P.O. Box 271, La Jolla, California 92038

Numerous (84) acoustic detections of singing humpback whales were made during a spring (08 March–09 June 1997) research cruise to study sperm whales in the central and eastern North Pacific. Over 15 000 km of track-line was surveyed acoustically using a towed hydrophone array. Additionally, 83 sonobuoys were deployed throughout the study area. Detection rates were greatest in late March, near the Hawaiian Islands, and in early April, northeast of the islands. Only one detection was made after April. Detection rates for sonobuoys were unequal in three equally divided longitudinal regions of the study area. Two high density clusters of detections occurred approximately 1200–2000 km northeast of the Hawaiian Islands and were attributed to a large aggregation of migrating animals. The distribution of these detections corroborates findings of previous studies. It is possible that these animals were maintaining acoustic contact during migration. Two unexpected clusters of singing whales were detected approximately 900 to 1000 km west of central and southern California. The location of these detections may indicate a previously undocumented migration route between an offshore breeding area, such as the Revillagigedo Islands, Mexico, and possible feeding areas in the western North Pacific or Bering Sea. © *1999 Acoustical Society of America.* [S0001-4966(99)03706-6]

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INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are undoubtedly the most studied of the large whales. In spite of this, little is known about their migratory routes, particularly in the North Pacific. In this study, numerous acoustic detections of singing humpback whales were made, revealing new information about the temporal, spatial, and behavioral characteristics of humpback whale migrations. Data were collected during a cruise conducted by the U.S. Southwest Fisheries Science Center (SWFSC) to study sperm whales (Barlow and Taylor, 1997). Fortunately, the timing and geographic area of the cruise coincided well with the northbound migration of humpback whales in the central and eastern North Pacific. This study was the first large-scale visual-acoustic survey of cetaceans in the eastern North Pacific and covered the greatest area ever surveyed using these techniques.

Humpback whales migrate annually from temperate and subpolar waters, where they feed in summer and fall, to tropical islands, coastal waters, and underwater banks, where they congregate to breed in winter through spring (Dawbin, 1966; Nishiwaki, 1966; Winn and Winn, 1978; Darling and McSweeney, 1985; Baker *et al.*, 1986). In fact, humpback whales have the longest mammalian migration ever documented (Clapham, 1996; Stone *et al.*, 1990). Long, complex songs are sung only by males during breeding season (Winn *et al.*, 1973; Winn and Winn, 1978; Lambertsen *et al.*, 1988; Medrano *et al.*, 1994). The function of singing is not well understood (Helweg *et al.*, 1992). However, most researchers agree that the primary role of song for humpback whales is similar to that for many birds, an advertisement display to attract mates and to displace or deter competitors (Winn and Winn, 1978; Tyack, 1981; Tyack and Whitehead, 1983; Frankel *et al.*, 1995). Although humpback whale songs are most often recorded in shallow water, low-latitude, breeding areas, they also have been recorded at high latitude feeding areas (Matilla *et al.*, 1987; McSweeney *et al.*, 1989), in deep water (Tyack and Whitehead, 1983; Clapham and Mattila, 1990; Frankel *et al.*, 1995), and along migration routes (Kibblewhite *et al.*, 1966; Payne and McVay, 1971; Dawbin and Gill, 1991).

The acoustic characteristics of humpback whale songs (e.g., high-intensity, repetitive signals with low-frequency energy) make them detectable at distances of 9–32 km or more using hydrophones (Winn *et al.*, 1975; Levenson and Leapley, 1978; Winn and Winn, 1978; Frankel *et al.*, 1995). In deep water (>200 m), favorable propagation characteris-
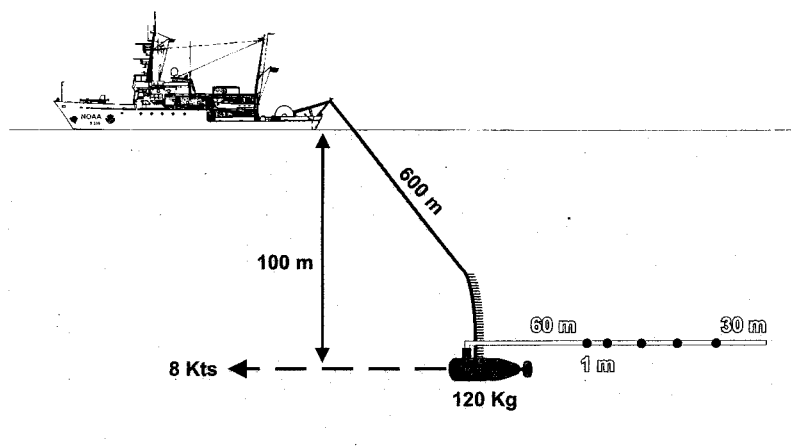

FIG. 1. Towed array acoustic system. The line with black circles (hydrophones) represents the towed array. The A/D converter and digital transmission system were encased in a pressure housing inside the towed-body. The black line (600 m) represents an oceanographic cable used to telemeter digital acoustic data to the ship.

tics and low ambient noise further increase the detection range of songs. Also, individual humpback whales often sing continuously for long periods (up to 24 h; Winn *et al.*, 1975) surfacing to breathe on average only every 14 minutes (Chu, 1988). Under these conditions, acoustic detections of singing animals are much more probable than visual detections.

Singing humpback whales have been acoustically surveyed and tracked in (or near) shallow water breeding areas using bottom-mounted hydrophone arrays, sonobuoys, and vessel deployed hydrophones (Winn *et al.*, 1975; Levenson and Leapley, 1978; Thompson and Friedl, 1982; Frankel *et al.*, 1995). Surveys of singing whales along potential humpback whale migratory routes were conducted by Clapham and Mattila (1990) in coastal and pelagic waters of the western North Atlantic, and by Dawbin and Gill (1991) along coastal waters off western Australia. In both of these studies, singing whales were detected using a single omnidirectional hydrophone deployed from a sailboat at ''recording stations.'' Although their results were limited in geographic scope (e.g., Winn *et al.*, 1975; Levenson and Leapley, 1978), or were constrained by the sampling design (e.g., nonrandom/systematic surveys; Clapham and Mattila, 1990; Dawbin and Gill, 1991), these researchers demonstrated that acoustic surveys of migrating humpbacks are effective.

More recently, Abileah *et al.* (1996) used beamformed data from the U.S. Navy's Sound Surveillance System (SOSUS) of hydrophone arrays in the North Pacific to detect singing humpback whales during their northbound migration across a large area north of Hawaii. They claimed to make over 100 detections during a 6-week period, but presented geographic locations for only six animals.

I. METHODS

Visual and acoustic surveys of cetaceans were conducted from 6 March through 10 June 1997 using NOAA's R/V MCARTHUR, a 52-m, oceanographic ship. The area and months of study were chosen to cover a large region of potential sperm whale habitat in the eastern North Pacific during their breeding season (Barlow and Taylor, 1997). Transect lines were placed systematically (given the con-

straints of the vessel's range) within the study area so that equal coverage occurred in four (N, S, E, W) equally divided quadrants.

Line transect sampling techniques (Buckland *et al.*, 1993) were used to visually survey all species of cetaceans encountered. NOAA/SWFSC marine mammal survey protocol (Barlow, 1995) was followed (with the exception that survey speed was reduced slightly to 7–8 kts to accommodate a towed array).

A towed hydrophone array system was incorporated into the survey to enhance detections of sperm whales. Sperm whales dive for long durations, making it difficult to detect them visually (Barlow, 1994, 1995). However, they consistently produce bioacoustic signals, and thus can be detected effectively using passive acoustics. During daylight hours, visual and acoustic surveys were conducted concurrently, but independently, to prevent acoustic and visual ''observers'' from cueing each other, and also to give both observer platforms the same opportunity to detect animals.

The towed hydrophone array system was designed primarily for detecting and determining bearings to sperm whale ''clicks.'' System frequency response was flat from approximately 10 to 16 000 Hz. Therefore, the system was capable of adequately receiving humpback whale songs which typically contain energy from 60 to 8000 Hz with dominant frequencies below 500 Hz (Levenson, 1969, 1972; Norris, 1995).

The hydrophone array (solid ''stealth'' array by ITI, Fort Worth, TX) consisted of five elements, irregularly spaced between 1 and 8 m. Two of the five hydrophones were selected electronically for digital transmission of acoustic data to the ship (Geo-Acoustics telemetry system, Ontario, Canada). Signals from these two channels were sampled at 32 kHz. The digital telemetry system and interface circuitry was housed in a 140-kg towed fish (originally designed for a towed sonar system) that was maintained at approximately 100-m depth (Fig. 1). This system was designed to be towed at near-normal marine mammal survey speeds, and at a suitable depth and distance from the ship to minimize ship noise. Gain-enhancing signal processing (e.g., beamforming) was not used.

On the ship, both channels were converted back to analog signals (effectively low-pass filtering at 16 kHz). The

signal from one channel was high-pass filtered at 1 kHz to reduce system, ship, and flow noise. Custom written spectrographic software displayed signals in real-time on a video monitor [Fig. 2(a)]. Signals from the other channel were high-pass filtered at a corner frequency of 10 Hz so that low-frequency signals produced by baleen whales could be detected.[1] Signals from both channels were input to a stereo headset for aural monitoring. Broadband signals were recorded continuously using a two-channel, DAT recorder (Sony DAT Walkman TCD-D8 or TCD-D7). Tapes which included signals of interest were saved for post-analysis and archival purposes.

Four acoustic technicians monitored signals from the towed array approximately 22 h per day. Detections of humpback whale song were noted on a computer file that stored and plotted GPS locations of the ship every 5 min (Barlow, 1997). A detection was defined as any signal heard (or seen) that exhibited characteristics unique to humpback whale song (e.g., frequency-modulated signals such as cries, moans, and whoops that are repeated in a rhythmic pattern). The following information was recorded: (1) presence/absence of humpback whale songs in a designated 20-min period each hour; (2) the estimated number of animals singing; (3) the time for any additional song detections during the remaining 40-min period; and (4) a subjective score of the signal-to-noise ratio (1–5 scale). These data were collected in order to standardize the signal monitoring and data recording effort, and to reduce the possibility of "double counting" the same animals (because only one detection was possible for any whale singing during each 1-h period). Song detections were included in the analysis only if at least one additional detection (from either the towed array or a sonobuoy) occurred in a 2-h period before or after the initial detection (4-h period total) or if the song detection was verified by a second bio-acoustician.

Sonobuoys (type 57A) were deployed each day (weather permitting) at a hydrophone depth setting of 122 m. Sonobuoys were used primarily to monitor for low-frequency signals produced by baleen whales, including songs of humpback whales. Occasionally, sonobuoy arrays (usually four to five sonobuoys) were deployed on groups of acoustically active sperm whales. Sonobuoy signals were transmitted to a multi-channel receiver (Greeneridge Sciences) and recorded on audio DAT [Sony DAT Walkman model TCD-D8 or TCD-D7, two channels at 48-kHz sampling rate; or a TEAC model RD135, up to eight channels at 20-kHz sampling rate; Fig. 2(b)]. Sonobuoys also were deployed when large cetaceans were encountered. Sonobuoy signals were recorded for at least 40 min or until the signal quality was considered unacceptable. Short (approximately 1 min.) signal segments were acquired in real-time every few minutes and spectrographs were produced (using Canary bio-acoustical signal processing software) for visual inspection. If humpback whale songs were not detected during shipboard monitoring, DAT recordings were reviewed later by examining spectrograms made from 3-min segments of signals extracted from every 5–10 min of tape.
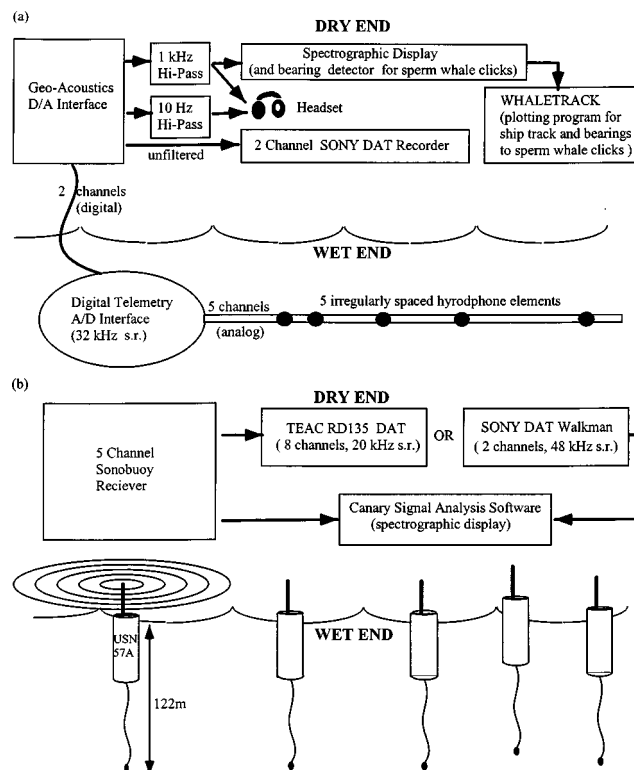

FIG. 2. (a) Towed hydrophone-array system. The digital telemetry system (housed in towed fish) was used to select signals from two hydrophones for digital transmission to the dry end. (b) Sonobuoy recording system. Up to five sonobuoys could be recorded simultaneously; however, usually only one or two were deployed at a time.

II. RESULTS

Approximately 15 400 km of track-line were acoustically surveyed with the towed array for a total of 1040 hours of effort (Fig. 3). Detection rates of humpback whale songs were greatest during leg I, 08 March–03 April (0.184 detections/hour), somewhat lower during leg II, 08 April–07 May (0.110), and lowest during leg III, 11 May–09 June (0.002). Detection rates for the towed array were unequal among the three legs ($X^2 = 58.64$; $df = 2$; $p < 0.05$). Songs were not detected after 23 May.

Humpback whale songs were detected on 30% (21 of 83) of all sonobuoys deployed over 64 days. Sonobuoy detection rates (buoys with detections/buoys deployed) were 0.423 during leg I and 0.357 during leg II. There were no detections from sonobuoys during leg III. Sonobuoy detection rates were unequal when compared among the three legs ($X^2 = 11.51$; $df = 2$; $p < 0.05$).

Overall, songs were detected on 34% (19 of 56) of days in which there was acoustic effort with the towed array, and on 28% (18 of 64) of days with at least one sonobuoy deployment. Combined, the sonobuoys and towed array resulted in detections of singing humpback whales on 36% (23 of 70) of days with acoustic effort. In comparison, only four visual sightings of humpback whales were made during 77 days (690 hours) of effort (Table I).

Detection rates of sonobuoys were unequal when compared among three equally divided longitudinal sectors of the study area ($X^2 = 24.13$; $df = 2$; $p < 0.05$; Table II). The high-

TABLE I. Summary of effort and number of humpback whale song detections per leg. Towed array detections of songs are indicated as the number of effort days and hours with at least one detection. Sonobuoy detections are indicated by the number of sonobuoys in which at least one detection of song was made. Visual detections were widely separated in space and/or time.

	Effort				Detections			
Leg no. (dates)	Days at sea	Towed array km (h)	Sonobuoys deployed	Visual km (h)	Towed array days with detection	Towed array hours with detection	Sonobuoys	Visual
Leg I 08 March–03 April	24	2581 (174)	26	3070 (207)	5	32	11	1
Leg II 07 April–07 May	30	6865 (463)	28	3531 (238)	11	51	10	2
Leg III 11 May–09 June	28	5998 (404)	29	3627 (244)	1	1	0	1[a]
Total	82	15 565 (1041)	83	10 228 (689)	17	84	21	4

[a]Mother with calf.

est densities of detections occurred in the vicinity of the Hawaiian Islands, especially during the first NE transect of leg II (Fig. 1). Additionally, there were two distinct clusters of detections located 900–1000 km off the coast of southern and central California at approximately 30° N 130° W and 36°N 134° W, respectively (Fig. 2). These two clusters of detections were separated (due to the timing of the survey legs) by 48 days.

III. DISCUSSION

A. Temporal and spatial distribution

Greater song detection rates occurred during late March and early April compared to mid April through early June. Although these temporal trends may have been partially biased due to the high densities of singing animals encountered near the Hawaiian Islands during the end of leg I and the beginning of leg II, these results are supported by findings from other studies on relative abundances and the timing of the northbound migration of humpback whales in the Hawaiian Islands (Baker and Herman, 1981; Smultea, 1994; Mate et al., 1998). Only one song detection was made after 30 April (approximately 1400 km north of the Hawaiian Islands on 23 May, leg III; Fig. 2). Late April generally denotes the end of the humpback whale winter/breeding season in the North Pacific, as most humpback whales have departed north to feeding areas (Herman et al., 1980; Baker and Herman, 1981). The low detection rate for leg III may have been due to a decrease in singing behavior, a reduction in the number of animals present, or most likely, a combination of these.

Relative abundances of humpback whales at, or near, breeding areas and along migration routes have been shown to be temporally staggered with respect to age/sex classes

(Nishiwaki, 1966; Dawbin, 1966, 1997; Smultea, 1994; Gabrielle, 1992; Brown et al., 1995). Reproductively mature males (e.g., singers) and females depart after newly pregnant and nonreproducing females, but before females with newborn calves. As long as these age- and sex-class-related differences are accounted for, acoustic surveys can be used for examining the migratory behavior of reproductively active males, and even the timing of migration for non-singing whales.

The densities of song detections were unequally distributed with respect to three equal longitudinal sectors (Table II). As expected, the greatest densities of singers occurred near the main Hawaiian Islands (Fig. 3). Song detections were scattered broadly to the northeast and northwest of Oahu, areas where survey effort was concentrated. High densities of singing animals were detected during leg II at the northeast end of the first transect (originating in Oahu heading NE). Presumably, these animals were migrating to Alaskan feeding areas (Calambokidis et al., 1997; Baker et al., 1986). During late March and early April 1995, Mate et al. (1998) tracked the initial northbound migration of four humpback whales (a female with calf, an adult, and a possible juvenile) tagged with satellite transmitters in waters off Kauai. The adult and the smaller animal (juvenile) traveled over 1600 and 1800 km, respectively, on a heading of approximately magnetic north (10° true) before the signal was lost. At the same time, Abileah et al. (1996) used cross-fixing techniques with SOSUS hydrophone arrays to determine the locations of singing humpback whales in the same region. They determined four locations between approximately 30 N and 40 N which they used to ''loosely define a 'migration corridor' bounded by longitudes 150 W and 160 W.'' Although the distribution of detections from leg II of

TABLE II. Sonobuoy detections by longitudinal sectors with expected distribution if randomly distributed.

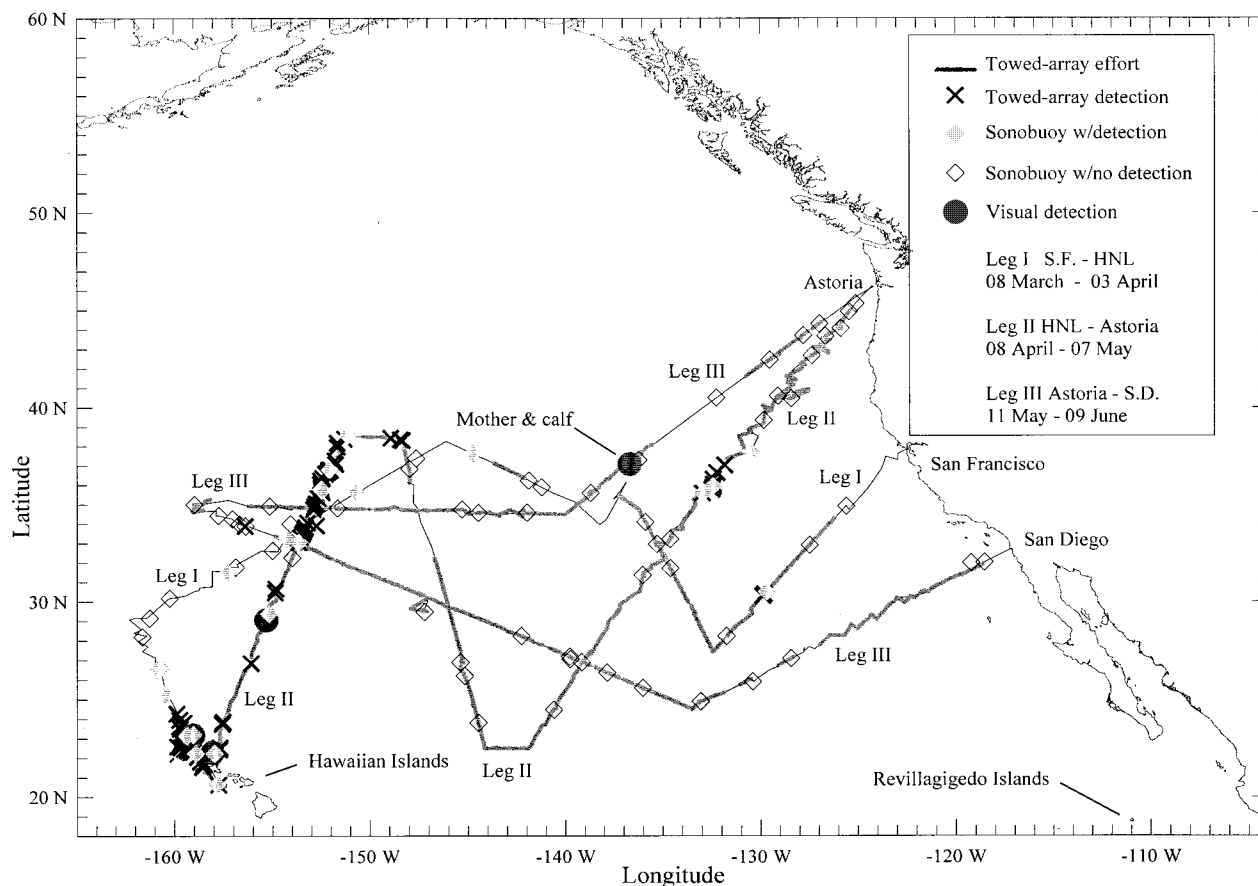|	Longitudinal sector			
	164W–150W	149W–135W	134W–120W	Total
No. of sonobuoys deployed	61	73	81	215
No. of sonobuoys with detections	16	1	4	21
No. of detections expected if random	5.96	7.13	7.91	21

FIG. 3. Locations of acoustic and visual detections of humpback whales. Acoustic detections are not necessarily representative of individual animals (e.g., one individual may be represented by more than one ×). Towed array effort depicted by thick track lines.

our study corroborates these findings (Fig. 1), there also were numerous detections made during the end of leg I (NNE of Oahu) that were outside of boundaries of their "migration corridor." However, most of these detections occurred earlier in the season and, generally, were within 200 km of the Hawaiian Islands.

The large group of acoustic detections that occurred to the northeast of Oahu (approximately 33°–38° N; Fig. 2) in mid-April can be attributed to a disperse group of singing animals migrating within general proximity (tens of miles) of each other. Assuming that these animals were traveling at similar rates and headings, this "pulse" of detections could have been the result of a concentration of animals that departed the Hawaiian Islands within a short period (e.g., a few days). Payne and Webb (1971) proposed that baleen whales may maintain acoustic contact over large areas (e.g., ocean basins) forming what they termed a "range herd." It is possible that singing may be used by a group of humpbacks to maintain contact during migrations. Alternatively, it also is possible that these high-density regions of singing whales are an indication that courtship activity continues during migration. To examine these possibilities will require information about the behavior of both singing males and nonsinging females during migration.

Perhaps of greater interest were two clusters of detections that occurred approximately 900–1000 km off the coast of California (Fig. 3). This band of pelagic detections was not associated with islands, seamounts, or any other obvious seabed features that might indicate a previously unknown breeding area for humpback whales in North Pacific. To our knowledge, there is no other documented information about sightings or acoustic detections of humpbacks whales from this offshore region.

Humpback whales have been detected off the California coast during winter and spring from aerial surveys (Dohl et al., 1983; Forney et al., 1995) and from photographic identification studies (Calambokidis et al., 1996). Based on aerial surveys off California, Forney and Barlow (1998) determined that winter/spring sightings of humpback whales were distributed significantly further offshore than summer/ fall sightings. They suggested the possibility that offshore winter/spring animals "are traveling through the offshore region en route to other feeding areas to the north." Unfortunately, in all of these studies, surveys were limited to waters within 100 nautical miles (180 km) of the coast (Forney et al., 1995), or within the continental shelf break (Dohl et al., 1983; Calambokidis et al., 1996).

Calambokidis et al. (1996) collected photographic identifications of humpback whales (597 individuals) from nearshore waters (<65 km) off California, Washington, and Oregon, from April through December. These were compared to an extensive photographic catalog of whales (>700 individuals) from eastern North Pacific feeding areas (British Columbia, Canada, SE Alaska, Prince William Sound, Ko-
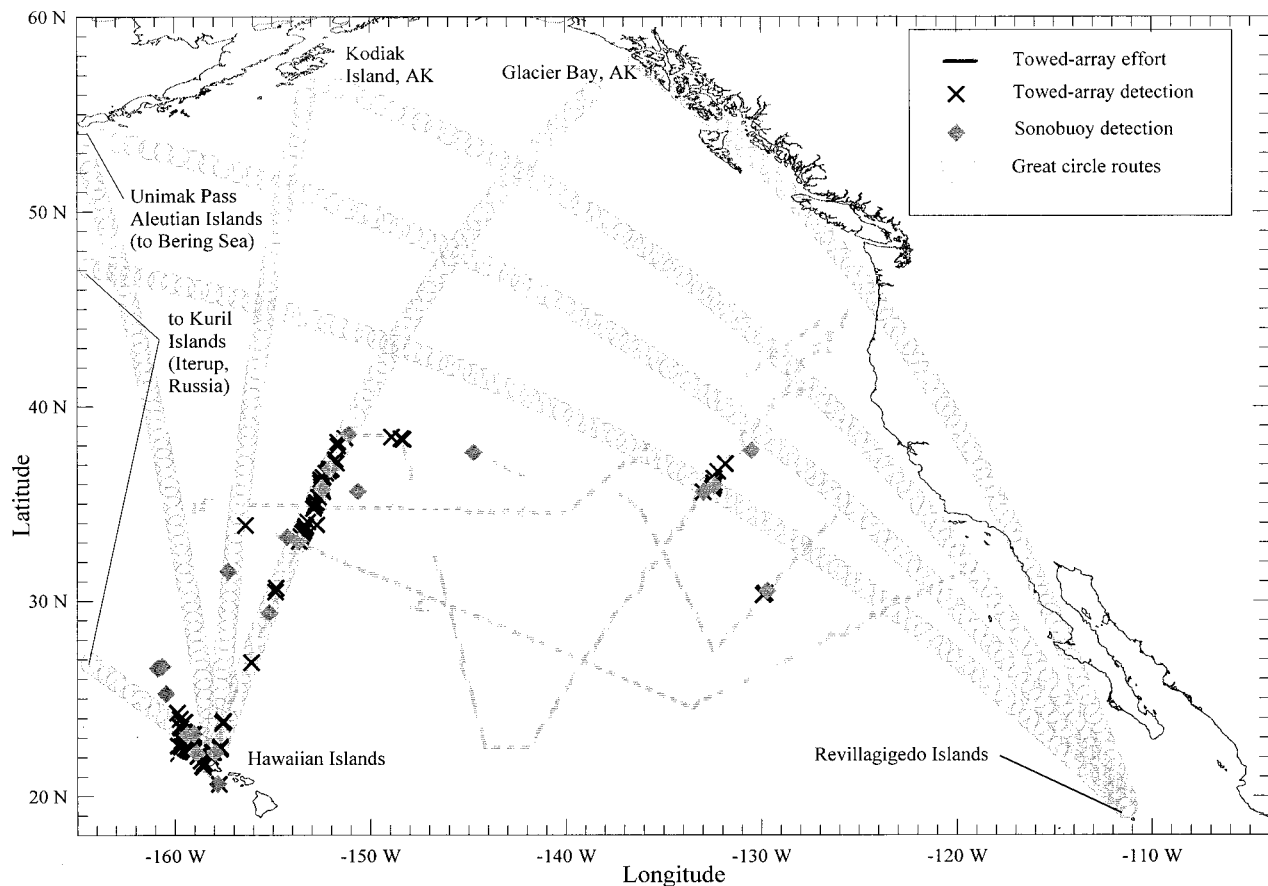
FIG. 4. Locations of all humpback whale acoustic detections with great circle routes plotted from the Hawaiian and Revillagigedo Island breeding areas to possible North Pacific feeding areas. Routes were not plotted from Hawaii to CA/OR/WA and BC (Canada) feeding areas because there is limited interchange of animals between these locations (Baker *et al.*, 1986; Calambokidis *et al.*, 1997). Great circle routes are not intended to indicate the actual paths taken by migrating whales, only possible termini.

diak Island and Shumigan Island, AK, and the Bering Sea). The paucity of matches between these two data sets led them to conclude that the waters off CA/WA/OR represented a distinct feeding area, and that animals bound for Alaskan waters (from Mexico) must "migrate well offshore (more than 65 km), or pass earlier or later in the season than [their] sampling effort." Only one[2] match was found when a photographic identification catalog of humpback whales from the Revillagigedo Islands (159 individuals) was compared with those from a large (1000 individuals) catalog of whales from numerous eastern North Pacific feeding areas (Calambokidis *et al.*, 1997).

B. Implications for migratory routes

One explanation for the clusters of detections discovered offshore of California is that they represent singing animals that were migrating north from wintering/breeding areas off Mexico.[3] Furthermore, the great distance that these detections occurred from shore could indicate that these animals originated from an offshore breeding area such as the Revillagigedo Islands (Fig. 4). If these offshore detections were indeed from migrating animals that originated from the Revillagigedo Islands, whereas individuals from the Mexican mainland breeding areas are following a more coastal migration route (as appears to be the case; Calambokidis *et al.*,

1996), then there may be evidence for segregation of migration routes for humpback whales from two geographically close, but separate, breeding areas. This situation would have great implications concerning the population structure of North Pacific humpback whales. To examine these possibilities will require determining the migration routes taken by humpback whales from different breeding areas (especially those from Mexican and Japanese waters) and determining differences in migratory behaviors related to age class, sex class, and reproductive status.

Possible migratory destinations of singing humpback whales detected in this study were investigated by plotting great circle routes (i.e., the shortest possible route between two points on a globe) between Hawaiian and Revillagigedo Island breeding areas, to potential feeding areas in the North Pacific. The great circle routes (GCR) that originate from the Revillagigedo Islands and pass through the offshore cluster of detections, lead to areas in the western North Pacific or Bering Sea (e.g., the western Aleutian Islands, Kamchatka Peninsula, or Kuril Islands; Fig. 4). Obviously, plotting GCR is an oversimplified prediction of possible endpoints of migrations, and, as such, they are not meant to indicate the actual routes taken by migrating whales.

There has been limited photographic identification effort in the western North Pacific and Bering Sea. However, the

paucity of matches for whales between the Revillagigedo Islands and several well-documented feeding areas in the eastern North Pacific has led some investigators to suggest that humpback whales from the Revillagigedo Islands breeding area could be migrating to feeding areas in the western North Pacific or Bering Sea (Calambokidis et al., 1997).

Although it cannot be ruled out, it is unlikely that the offshore cluster of detections were ''Hawaiian'' animals migrating to coastal feeding areas off California, Oregon, and Washington. All of these areas have been sampled thoroughly from photographic identification studies and results indicate limited interchange of animals (Perry et al., 1988; Calambokidis et al., 1997). There were no detections of humpback whales in the region between the offshore cluster of detections and the U.S. coast (i.e., the end of leg II and the beginning of leg III), a region that had excellent acoustic and visual coverage (Fig. 2). Therefore, it is unlikely that the offshore detections were of animals migrating from Mexican breeding areas to feeding areas in SE Alaska or the mainland U.S. coasts.

If, in fact, whales from the Revillagigedo Islands are migrating to feeding areas in the western Pacific or Bering Sea, the resulting implications are considerable. For example, humpback whales migrating between from the Hawaiian Islands and SE Alaska (and adjacent feeding areas; Baker et al., 1986) and those animals migrating between the Revillagigedo Islands and western North Pacific feeding areas would cross paths in a broad region several hundred miles northeast of the Hawaiian Islands (approximately 45° N, 145° W; Fig 3). If this scenario is correct, it could explain when and where acoustic contact between singing whales is occurring, and how animals in acoustically isolated breeding regions (Mexico and Hawaii) are maintaining a similar, yet changing, version of song [Winn et al., 1981; Payne and Guinee, 1983; Helweg et al., 1992, 1998; Cerchio et al. (in press)]. The evolutionary implications of segregated but crossing migration routes for these putative stocks of whales are quite significant, however further examination of these must await substantiation of actual migration routes and an assessment the degree of reproductive isolation for animals from different breeding areas.

Recent information from photographic identification studies indicates that some humpback whales migrate between feeding and breeding areas that are on opposite (i.e., diagonally opposed) ends of their respective ocean basins (e.g., Japan to British Columbia, Canada, for North Pacific humpback whales; Darling et al., 1996; and Norway to the West Indies for North Atlantic humpback whales; Stevick et al., 1998). Some researchers have even speculated that humpback whales could be taking advantage of ''tail-currents'' in the North Pacific (Baker and Herman, 1981); others, however, have discounted this possibility for humpback whale migrations occurring in the northern (Mate et al., 1998) and southern hemispheres (Dawbin, 1966).[4]

C. Biases, recommendations, and conclusions

In this study, systematic transects were used to survey a large study area. By coincidence, several transects were oriented parallel to the direction of migrating humpback

whales. Unfortunately, in one case (e.g., the first transect of Leg II), the survey vessel was traveling in the same direction as migrating whales (Fig. 2). A more effective sampling design for humpback whales would consist of systematic transects that are arranged perpendicular (e.g., east–west) to the predominant direction of travel (e.g., south–north) for migrating whales. Another potential bias of this study was the poor towed array coverage (due to equipment malfunctions and weather constraints) of coastal regions off the western continental U.S. and NW of the Hawaiian Islands (Fig. 3). This precluded an assessment of the coastal distribution of singing/migrating humpback whales and potentially biased the trends observed near the Hawaiian islands (although sonobuoy coverage was adequate there).

To effectively use acoustic surveys to determine absolute abundances of animals, it will be necessary to determine the proportion of time animals spend singing (or producing other sounds). In humpback whales, song bout length increases throughout the breeding season (Tyack, 1981), and it is likely that bioacoustical signals produced by other mysticetes vary temporally as well. To asses this potential bias, numerous individuals must be acoustically monitored for extended periods (e.g., hours to days). This will require visually tracking or tagging animals while simultaneously monitoring their acoustic behavior. Fortunately, recent advances in tagging and tracking techniques will probably allow these data to be collected in the near future (Flagg et al., 1997; Fletcher et al., 1996; Frankel, 1995). Until then, acoustic surveys will be limited to describing *relative* distribution and abundances of bioacoustically active animals.

Another problem associated with acoustic survey techniques is the difficulty in reliably determining an estimate of the absolute number of animals detected based on acoustic ''contacts'' (Hiby and Hammond, 1989; Thomas et al., 1986; Leaper et al., 1992). In this study, the total number of hourly periods with song detections is most likely an overestimate of the actual numbers of singing animals encountered because, on average, each individual was probably detected more than once (i.e., in more than one hourly period). Conversely, the number of days with acoustic detections is a great underestimate of the actual number of animals encountered, because acoustic detections often occurred in clusters, resulting in no more than one detection counted for any group of animals (Fig. 2). Because the acoustic system in this study was not designed to localize individual whales, a statistically based estimate (e.g., using distance sampling methods) of the abundance of singing whales could not be made.

Probably the most important recommendation for future acoustic surveys is to incorporate sound source localization techniques so that the absolute number of animals encountered can be estimated more accurately. Localization with towed arrays is possible using signal arrival delays (Barlow, 1997), beamforming (Lashkari and Lowder, 1997), and hyperbolic fixing (Clark and Fristrups, 1997), or (using a more simplistic approach) with directional hydrophones (Leaper et al., 1992; Winn et al., 1975). Given their field-proven effectiveness, acoustic detection systems should be included as

an important component in future studies of the distribution, relative abundance, and behavior of bio-acoustically active cetaceans.

Results from this study provided new information on migratory routes of humpback whales across a large region of the eastern North Pacific. Future studies should examine migratory routes of animals from isolated breeding areas, the extent that singing occurs during migration, and differences in migratory behaviors related to differences in age, sex, and reproductive classes.

ACKNOWLEDGMENTS

[1]Due to flow noise, ship noise, and natural ambient noise, most faint biological signals were note detectable at frequencies below 100 Hz.

[2]The Revillagigedo Island photographic sample used in this study was collected during only 1 season (compared to at least three seasons for most other areas). Recently, Jorge Urban and Jeff Jacobsen (personal comm.) have found additional matches between animals from the Revillagigedo breeding area and Alaskan feeding areas. However, the rate of matches still remains low (<5%).

[3]Most data indicates that in the Mexican Pacifc there probably are two isolated stocks of whales: a coastal mainland stock and a stock around the Revillagigedo Islands (Urban *et al.*, 1987; Alvarez *et al.*, 1988).

[4]It is interesting to note that a southeast–northwest migration route from the Revillagigedo Islands would bypass the California Current (southerly flow). If this route were to continue towards northeastern Asia, it might allow animals to take advantage of the Alaskan Stream (westerly flow) and Kamchatka Currents (southwesterly flow).

Abileah, R., Martin, D., Lewis, S. D., and Gisiner, B. (**1996**). ''Long-range acoustic detection and tracking of the Hawaii-Alaska migration,'' in MTS/IEEE Oceans 96, Ft. Lauderdale, FL, Vol. 1, pp. 373–377.

Alvarez, C., Aguayo, A., Rueda, R., and Urban, J. (**1988**). ''A note on the stock size of humpback whales along the Pacific coast of Mexico,'' Rep. Int. Whal. Commn. (special issue 12): 191–193.

Baker, C. S., and Herman, L. M. (**1981**). ''Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters,'' Can. J. Zool. **59**, 461–469.

Baker, C. S., Herman, L. M., Perry, A., Lawton, W. S., Straley, J. M., Wolman, A. A., Kaufman, G. D., Winn, H. E., Hall, J. D., Reinke, J. M., and Ostman, J. (**1986**). ''Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific,'' Mar. Ecol. Prog. Ser. **31**, 105–119.

Barlow, J. (**1994**). ''Recent information on the status of large whales in California,'' NOAA Tech. Mem. NMFS-SWFSC-203, Southwest Fisheries Science Center, La Jolla, CA.

Barlow, J. (**1995**). ''The abundance of cetaceans in California waters. Part I: ship surveys in summer and fall 1991,'' Fish. Bull. **93**(1), 1–14.

Barlow, J. (**1997**). ''SWAPS cruise towed acoustic system,'' unpublished report, NOAA Southwest Fisheries Science Center, La Jolla, CA.

Barlow, J., and Taylor, B. (**1997**). ''Acoustic census of sperm whales in the eastern temperate North Pacific,'' J. Acoust. Soc. Am. **102**, 3213 (abstract).

Brown, M. R., Corkeron, P. J., Hale, P. T., Schultz, K. W., and Bryden, M. M. (**1995**). ''Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*)'' Proc. R. Soc. London, Ser. B **259**, 229–234.

Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (**1993**). *Distance Sampling: Estimating Abundance of Biological Populations* (Chapman and Hall, London).

Calambokidis, J., Steiger, G. H., Evenson, J. R., and Flynn, K. R. (**1996**). ''Interchange of humpback whales off California and other North Pacific feeding grounds,'' Mar. Mamm. Sci. **12**(2), 215–226.

Calambokidis, J., Steiger, G. H., Straley, J. M., Quinn II, T. J., Herman, L. M., Cerchio, S., Salden, D. R., Yamaguchi, M., Sato, F., Urban, R., Jacobsen, J., von Ziegesar, O., Balcomb, K. C., Gabriele, C. M., Dahlheim, M. E., Higashi, N., Uchida, S., Ford, J. K. B., Miyamura, Y., Ladron de Guevara, P. P., Mizroch, S. A., Schlender, L., and Rasmussen, K. (**1997**). ''Abundance and population structure of humpback whales in the north Pacific basin,'' final report submitted to Southwest Fisheries Science Center, La Jolla, CA, Contract No. 50ABNF500113.

Cerchio, S., Jacobsen, J. K., and Norris, T. F. (**1999**). ''Temporal and geographic variation in songs of humpback whales (*Megaptera novaeangliae*): Synchronous change in Hawaiian and Mexican breeding assemblages,'' Behav. Ecol. Sociobiol. (in press).

Chu, K. C. (**1988**). ''Dive times and ventilation patterns of singing humpback whales (*Megaptera novaeangliae*),'' Can. J. Zool. **66**, 1322–1327.

Clapham, P. J. (**1996**). ''The social reproductive biology of Humpback Whales: an ecological perspective,'' Mamm. Rev. **26**, 27–49.

Clapham, P. J., and Matilla, D. K. (**1990**). ''Humpback whale songs as indicators of migration routes,'' Mar. Mamm. Sci. **6**(2), 155–160.

Clark, C. W., and Fristrup, K. M. (**1997**). ''Whales '95: A combined visual and acoustic survey of blue and fin whales off southern California,'' Rep. Int. Whal. Commn. **47**, 583–600.

Darling, J. D., and McSweeny, D. (**1985**). ''Observations of the migrations of North Pacific humpback whales (*Megaptera novaeangliae*),'' Can. J. Zool. **63**, 308–314.

Darling, J. D., Calambokidis, J., Balcomb, K. C., Bloedel, P., Flynn, K., Mochizuki, A., Mori, K., Sato, F., Suganuma, H., and Yamaguchi, M. (**1996**). ''Movement of a humpback whale (*Megaptera novaeangliae*) from Japan to British Columbia and return,'' Mar. Mamm. Sci. **12**(2), 281–287.

Dawbin, W. H. (**1966**). ''The seasonal migratory cycle of humpback whales,'' in *Whales, Dolphins and Porpoises*, edited by K. S. Norris (Univ. of California, Berkeley, CA), pp. 145–170.

Dawbin, W. H. (**1997**). ''Temporal segregation of humpback whales during migration in southern hemisphere waters,'' Memoirs of the Queensland Museum. **42**(1), 105–138.

Dawbin, W. H., and Gill, P. C. (**1991**). ''Humpback whale survey along the west coast of Australia: a comparison of visual and acoustic observations,'' Memoris of the Queensland Museum **30**(2), 255–257.

Dohl, T. P., Guess, R. C., Duman, M. L., and Helm, R. C. (**1983**). ''Cetaceans of central and northern California, 1980–1983: Status, abundance and distribution,'' OCS study MMS 84-0045, MMS Contract No. 14-12-0001-29090.

Flagg, M., Norris, T. F., and Croll, D. (**1997**). ''An acoustic transponder based tracking, data-telemetry, and logging system for real-time monitoring of 3-D positions and collection of other data from large marine vertebrates,'' J. Acoust. Soc. Am. **102**, 2462–3216.

Fletcher, S., LeBoeuf, B. J., Costa, D. P., and Tyack, P. L. (**1996**). ''Onboard acoustic recording from diving elephant seals,'' J. Acoust. Soc. Am. **100**, 2531–2539.

Forney, K. A., Barlow, J., and Carreta, J. V. (**1995**). ''The abundance of cetaceans in California waters. Part II: Aerial surveys in winter and spring of 1991 and 1992,'' Fish. Bull. **93**, 15–26.

Forney, K., and Barlow, J. (**1998**). ''Seasonal patterns in the abundance and distribution of California cetaceans, 1991–92,'' Mar. Mamm. Sci. **14**(3), 460–489.

Frankel, A. S., Clark, C. W., Herman, L. M., and Gabriele, C. M. (**1995**). ''Spatial Distribution, Habitat Utilization, and Social Interactions of Humpback Whales, *Megaptera novaeangliae*, off Hawai'i using Acoustic and Visual Techniques,'' Can. J. Zool. **73**(6), 1134–1146.

Gabriele, C. M. (**1992**). ''The behavior and residence characteristics of reproductive classes of humpback whales (*Megaptera novaeangliae*) in the Hawaiian Islands,'' M. S. thesis, University of Hawaii.

Helweg, D. A., Frankel, A. S., Mobley, Jr., J. R., and Herman, L. M. (**1992**). ''Humpback whale song: our current understanding,'' in *Marine Mammal*

Sensory Systems, edited by J. Thomas, R. Kastelein, and A. Supin (Plenum, New York), pp. 459–483.

Helweg, D. A., Cato, D. H., Jenkins, P. F., Garrigue, C., and McCauley, R. D. (**1998**). ''Geographic variation in South Pacific humpback whale songs,'' Behaviour **135**, 1–27.

Herman, L. M., Forrestell, P. H., and Antinoja, R. C. (**1980**). ''Study of the 1976/1977 migration of humpback whales into Hawaiian waters: composite description,'' Final Report to the U.S. Mar. Mamm. Commn. Report No. MMC-77/19, NTIS (PB80-162332, Arlington, VA.

Hiby, A. R., and Hammond, P. S. (**1989**). ''Survey techniques for estimating abundance of cetaceans,'' Behaviour Rep. Int. Whal. Commn. (special issue) **11**, 47–80.

Jacobsen, J., and Urban, Jorge (**1999**). Personal communication.

Kibblewhite, A. C., Denham, R. N., and Barnes, D. J. (**1966**). ''Unusual low frequency signals observed in New Zealand waters,'' J. Acoust. Soc. Am. **41**, 644–655.

Lambertsen, R. H., Baker, C. S., Duffield, D. A., and Chamberlin-Lea, J. (**1988**). ''Cytogenetic determination of sex among individually identified humpback whales (*Megaptera novaeangliae*),'' Can. J. Zool. **66**, 1243–1248.

Lashkari, K., and Lowder, S. (**1997**). ''Ocean Acoustic Observatory for PassiveMonitoring of the Ocean'' (abstract) Underwater Bio-Sonar and Bioacoustics Symposium, Loughborough, England, Vol. 19, Pt. 9, pp. 107–114.

Leaper, R., Chappel, O., and Gordon, J. (**1992**). ''The development of practical techniques for surveying sperm whale populations acoustically,'' Rep. Int. Whal. Commn. **42**, 549–560.

Levenson, C. (**1969**). ''Behavioral, physical, and acoustic characteristics of humpback whales (*Megaptera novaeangliae*) at Argus Island,'' Naval Oceanographic Office Informal Report No. 69–54.

Levenson, C. (**1972**). Characteristics of sounds produced by humpback whales (*Megaptera novaeangliae*), NAVOCEANO Tech. Note No. 7700-6-72 (Naval Oceanographic Office, Washington, DC).

Levenson, C., and Leapley, W. T. (**1978**). ''Distribution of humpback whales (*Megaptera novaeangliae*) in the Caribbean determined by a rapid acoustic method,'' J. Fish. Res. Board Can. **35**, 1150–1152.

Mate, B. R., Gisiner, R., and Mobley, J. (**1998**). ''Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry,'' Can. J. Zool. **76**, 863–868.

Matilla, D. K., Guinee, L. N., and Mayo, C. A. (**1987**). ''Humpback whale songs on the North Atlantic feeding grounds,'' J. Mammal. **68**, 880–883.

McSweeny, D. J., Chu, K. C., Dolphin, W. F., and Guinee, L. N. (**1989**). ''North Pacific humpback whale songs: a comparison of southeast Alaskan feeding ground songs with Hawaiian wintering ground songs,'' Mar. Mamm. Sci. **5**(2), 139–148.

Medrano, L., Salinas, M., Salas, I., Ladron de Guevara, P. L., Aguayo, A., Jacobsen, J., and Baker, C. S. (**1994**). ''Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering ground of the Mexican Pacific,'' Can. J. Zool. **72**, 1771–1774.

Nishiwaki, M. (**1966**). ''Distribution and migration of the larger cetaceans in the north Pacific as shown by Japanese whaling results,'' in *Whales, Dolphins and Porpoises*, edited by K. S. Norris (Univ. of California, Berkeley, CA), pp. 171–191.

Norris, T. F. (**1995**). ''The effects of noise on the singing behavior of humpback whales (*Megaptera novaeangliae*),'' M. S. thesis, Moss Landing Marine Laboratories, California State University.

Payne, R., and Guinee, L. (**1983**). ''Humpback whale (*Megaptera novaeangliae*) songs as an indicator of ''stocks,'' in *Communication and Behavior of Whales*, edited by R. Payne (Westview, Boulder, CO), pp. 333–358.

Payne, R. S., and McVay, S. (**1971**). ''Songs of humpback whales,'' Science **173**, 585–597.

Payne, R., and Webb, D. (**1971**). ''Orientation by means of long range acoustic signalling in baleen whales,'' Ann. (N.Y.) Acad. Sci. **188**, 110–142.

Perry, A., Baker, C. S., and Herman, L. M. (**1988**). ''Population characteristics of individually identified humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific: a summary and critique,'' Rep. Int. Whal. Commn. (special issue) **12**, 307–317.

Smultea, M. A. (**1994**). ''Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii,'' Can. J. Zool. **72**, 805–811.

Stevick, P. T. (**1998**). ''Migration of a humpback whale (*Megaptera novaeangliae*) between Norway and the West Indies,'' Mar. Mamm. Sci. **14**(1), 162–166.

Stone, G. S., Florez-Gonzales, L., and Katona, S. K. (**1990**). ''Whale migration record,'' Nature (London) **346**, 705.

Thomas, J. A., Fisher, S. R., and Ferm, L. M. (**1986**). ''Acoustic detection of cetaceans using a towed array of hydrophones,'' Rep. Int. Whal. Commn. (special issue) **8**, 139–148.

Thompson, P. O., and Friedl, W. A. (**1982**). ''A long term study of low frequency sounds from several species of whales off Oahu, Hawaii,'' Cetology **45**, 1–19.

Tyack, P. (**1981**). ''Interactions between singing Hawaiian humpback whales and conspecifics nearby,'' Behav. Ecol. Sociobiol. **8**, 105–116.

Tyack, P., and Whitehead, H. (**1983**). ''Male competition in large groups of wintering humpback whales,'' Behaviour **83**, 132–154.

Urbán, J., and Aguayo, A. (**1987**). ''Spatial and seasonal distribution of the humpback whale, *Megaptera novaeangliae*, in the Mexican Pacific,'' Mar. Mamm. Sci. **3**(4), 333–344.

Winn, H. E., Thompson, T. J., Cummings, W. C., Hain, J., Hudnall, J., Hays, H., and Steiner, W. W. (**1981**). ''Song of the humpback whale: population comparisons,'' Behav. Ecol. Sociobiol. **8**, 41–46.

Winn, H. E., Bischoff, W. L., and Taruski, A. G. (**1973**). ''Cytological sexing of cetacea,'' Mar. Biol. **23**, 343–346.

Winn, H. E., Edel, R. K., and Taruski, A. G. (**1975**). ''Population estimates of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques,'' J. Fish. Res. Board Can. **32**(4), 449–506.

Winn, H. E., and Winn, L. K. (**1978**). ''The song of the humpback whale (*Megaptera novaeangliae*) in the West Indies,'' Mar. Biol. **47**, 97–114.